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Experimental evidence for innate predator recognition in the Seychelles warbler

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Nest predation is a major determinant of fitness in birds and costly nest defence behaviours have evolved in order to reduce nest predation. Some avian studies have suggested that predator recognition is innate whereas others have stressed the importance of learning. However, none of these studies controlled for the genetic origin of the populations investigated and the effect of unfamiliarity with the predator. Here we determined whether experience with a nest predator is a prerequisite for nest defence by comparing predator recognition responses between two isolated but genetically similar Seychelles warbler (*Acrocephalus sechellensis*) populations, only one of which had experience of the egg predating Seychelles fody (*Foudia sechellarum*). Individuals in the predator-free population significantly reduced nest guarding compared to individuals in the population with the predator, which indicates that this behaviour was adjusted to the presence of nest predators. However, recognition responses (measured as both alarm call and attack rates) towards a mounted model of the fody were equally strong in both populations and significantly higher than the responses towards either a mounted familiar non-predator and a mounted, novel, non-predator bird species. Responses did not differ with a warbler's age and experience with the egg predator, indicating that predator recognition is innate.

Keywords: egg predation; nest defence behaviour; predator recognition; Seychelles warbler

1. INTRODUCTION

One of the most important direct determinants of fitness in birds is predation of their eggs or young (Lack 1954; Ricklefs 1969; Clark & Wilson 1981; Martin 1993; Poiani & Pagel 1997). Although nest defence by parents can reduce nest predation (e.g. Veen 1977; Greigh-Smith 1980; Knight & Temple 1986*a*), it is costly in terms of foraging time and energy expenditure (e.g. Biermann & Robertson 1983; Martin 1992), injury, death and reduced future reproductive success (e.g. Curio & Regelmann 1985; Nur 1988; Dijkstra *et al.* 1990). The optimal level of defence maximizes the difference between these fitness benefits and costs (e.g. Andersson *et al.* 1980; Curio *et al.* 1984; Knight & Temple 1986*a*; Montgomerie & Weatherhead 1988). Because the cost:benefit ratio varies with the age and experience of parents and also with the presence of predators, the intensity of nest defence should vary accordingly (Montgomerie & Weatherhead 1988; Redondo 1989; Forbes *et al.* 1994). The important components of nest defence are nest guarding (Martin 1992; Komdeur & Kats 1999), predator recognition and deterrence (Andersson *et al.* 1980). Nest guarding and predator recognition are of great importance because they result in a quicker and more specific reaction against intruders. Very few studies have been conducted on predator recognition in birds (Major & Kendal 1996). Some studies have suggested that predator recognition is innate ('no specific experience needed') (e.g. Tinbergen 1951; Curio 1969, 1975; Hobson *et al.* 1988), whereas others have stressed the importance of learning (Conover 1987; Thornhill 1989; Ferrer *et al.* 1990; McLean & Rhodes 1991). In addition, it is not known whether birds born in a predator-free environment have the ability to recognize nest predators and defend their nests accordingly. Here we differentiate between the innate and learned components of nest defence by comparing predator recognition responses between two isolated but genetically similar populations of Seychelles warblers (*Acrocephalus sechellensis*) (Komdeur *et al.* 1998), only one of which had experience with avian nest predators.

The cooperatively breeding Seychelles warbler is a rare island endemic in the Seychelles. Up until September 1988, when an additional breeding population was established on Aride Island (68 ha), it only occurred on Cousin Island (29 ha). The warbler populations on both islands are completely isolated from each other (Komdeur *et al.* 1998). The warblers are insectivorous and territorial throughout the year. Nest guarding and predator deterrence are highly adaptive on Cousin Island where the only egg predator of the warblers, the Seychelles fody (*Foudia sechellarum*), an endemic weaver bird, is abundantly present: egg predation from guarded nests is significantly lower than unguarded nests (Komdeur & Kats 1999). The fitness costs of egg predation are considerable because warblers usually have clutches of a single egg (91.0%) ($n = 223$), are single brooded with restricted breeding seasons and have reduced chances of a successful replacement clutch (Komdeur 1996). However, nest guarding is costly because of reduced foraging opportunities, resulting in lower body condition. The warbler shows great plasticity of nest guarding behaviour. Warblers that guarded their clutch on Cousin Island did not guard their clutch after translocation to Aride Island where egg-predating fodies are absent (Komdeur & Kats 1999).

The aim of this study was to test whether experience with the predator is a prerequisite for predator recognition

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in the Seychelles warbler. The transfer of warblers from Cousin Island, where fodies are present, to Aride Island, where there are no fodies, allowed us to test whether this was the case. On both islands we presented decoys of the Seychelles fody and the barred ground dove (*Geopelia striata*) close to a warbler's nest containing an egg in order to manipulate the risk of egg predation. The decoys were presented sequentially with the order alternating between nests. The barred ground dove, a non-predator which is common on both Cousin and Aride Islands, served as a control. If predator recognition is innate, we would expect warblers on Aride Island to respond differently to the two decoys, but react in the same way to the fody decoy as warblers on Cousin Island. If learning is important in shaping predator recognition, we would expect to see improved anti-predator behaviour with age. If so, the concomitant hypotheses are twofold: (i) an older warbler on Cousin Island which had had more encounters with Seychelles fodies should have a higher nest defence intensity, and (ii) nest defence should be absent on Aride Island where warblers have never experienced fodies. The responses toward a mounted great tit (*Parus major*), a novel non-predator, were scored in order to separate the effects of familiarity with the other two models from recognition of these models on defence intensity. In addition, by dividing the breeding pairs on both islands into age classes, we determined the effect of the duration of isolation from the egg predator on predator recognition.

2. MATERIAL AND METHODS

(a) *Study population and behavioural observations*

The Seychelles warblers were studied between May and August 1999 (the main breeding peak) (Komdeur 1996) on Cousin and Aride Islands. All birds studied were colour-ringed using a unique colour combination and were of known sex. All territories were checked for initiation of nest building by following females for 30 min (Komdeur 1992). During the nesting period, nests were checked for the presence of an egg or nestling every three days. One-hour observations on nest guarding (when the bird was perched < 2.5 m from the nest while the egg was not incubated) (Komdeur & Kats 1999) were conducted just before the experiments (see § 2(b)) during which total time nest guarding was recorded for each bird present in the territory. The size of territories and vegetation cover within territories were similar on both islands (Komdeur & Kats 1999).

(b) *Predator recognition experiment*

Predator recognition was measured as the difference in nest defence intensity shown against a mounted egg predator and a mounted non-predator present near the nest. In order to determine whether experience with a predator is a prerequisite for predator recognition, we calculated the difference in nest defence intensities between birds on Cousin (21 breeding pairs) and Aride (15 breeding pairs) Islands. The Seychelles fody is too rare to be sacrificed and mounted. Instead, we used a mounted female house sparrow for mimicking the fody (similar plumage coloration and pattern with $< 10\%$ difference in wing, tarsus and bill and 35% difference in weight) (Cramp *et al.* 1994; Kraaijeveld & Komdeur 2000). We also used a mounted barred ground dove which is a non-predator common on both islands (figure 1*b*). In order to test the accuracy of the house sparrow as a surrogate fody we presented a live fody in a cage to six breeding pairs (different from the 21 pairs mentioned above) on Cousin Island. A mounted great tit was used (figure 1*b*) for measuring responses towards a novel bird on Cousin Island only (fodies present) as the model was not available during the experiments on Aride Island.

All experiments were performed six to ten days after initiation of egg laying in order to control for the potential effects of clutch age on nest defence intensity (Curio 1975; Knight & Temple 1986*a*; Sjöberg 1994; but see Knight & Temple 1986*b*). The test consisted of sequential presentation of the sparrow, dove and tit attached to a pole and fixed at a distance of 0.4–0.6 m from the nest when no warbler was present near or on the nest. The presentation of the first model started immediately after the nest watch (see § 2(a)), the presentation of the second model *ca.* 24 h later and the third model *ca.* 48 h later. The order of presentation was randomly assigned for the first test and alternated for each subsequent test, thereby excluding habituation effects (Gottfried 1979; Maloney & McLean 1995). Observations on nest defence started after the first appearance of a warbler close to the nest and lasted 2 min (Weatherhead 1989; Hakkarainen & Korpimäki 1994; Meilvang *et al.* 1997). The identity of warblers present within 2.5 m of the model and defending the nest were recorded in the field and simultaneously filmed using a video camera (Sony Handycam 8 XR) which was mounted on a tripod and set up within 5–15 m of the model. The total numbers of attacks and calls were recorded in the field and verified using the video playback. An attack was defined as a peck on the model, which is essential in deterring a fody under natural conditions (Komdeur & Kats 1999). Attacking was the most costly nest defence trait measured (Montgomerie & Weatherhead 1988). The absence of a bird was noted as no response as the territories on both islands were relatively small thus enabling the warblers to hear each other within the territory (human observers can easily locate alarming warblers within the boundaries of a territory) (J. Komdeur, personal communication). The absence of warblers can therefore be regarded as a lack of interest in defending. The sequential test used in this study (comparing model-specific, provoked defence behaviour in the same territories) was an explicit matched-pairs design which controlled for group size and territory quality (expressed as insect food abundance) (Komdeur 1992).

(c) *Data analyses*

The nest guarding and nest defence data were not normally distributed, even after transformation and, therefore, were tested non-parametrically. Differences in the total nest guarding time of the males and females between both islands were analysed with the Mann–Whitney test. Helpers might affect the time spent nest guarding by the breeding pair by taking part in the nest guarding. Differences in nest guarding by Seychelles warblers with and without helpers were analysed using the Mann–Whitney test. Differences in defence intensity towards the different models and between the sexes were analysed with the Wilcoxon signed-rank test and differences between islands were analysed with the Mann–Whitney test. In order to test this, the sexes were pooled and a proportional measure for the difference between defence against the house sparrow and the barred ground dove (sparrow/(sparrow + dove)) was used. The effect of helpers was analysed with the Mann–Whitney test by dividing the territories into two groups (with and without helpers) and using the total response of the breeding male and female in the territory as a defence intensity measure. The

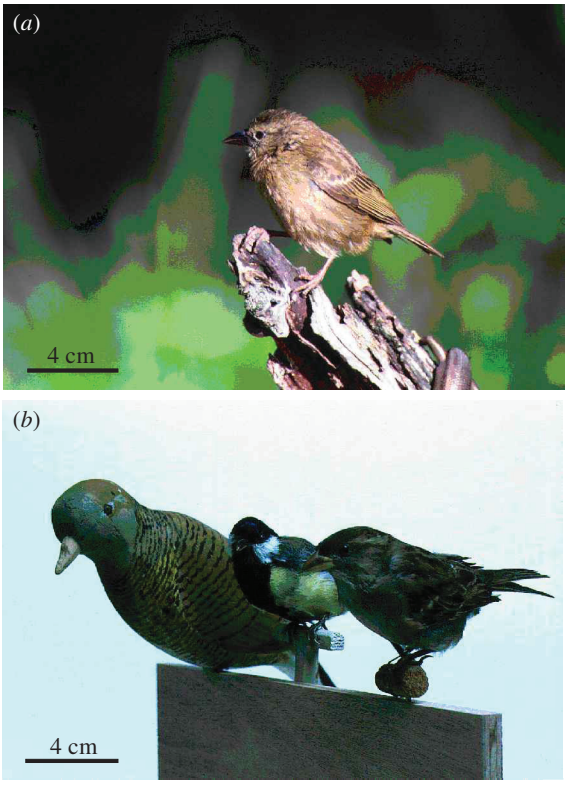

Figure 1. (*a*) The Seychelles fody. (*b*) The models used for the experiments (from left to right): the barred ground dove, the great tit and the house sparrow.

analysis showed that helpers had no influence on the defence intensity of the breeding pair (male and female combined, calls $U = 436.5$, $n = 72$ and $p = 0.512$, and attacks $U = 482.0$, $n = 72$ and $p = 0.954$). Helpers were therefore excluded from further analysis. The ages of the warblers were categorized into three classes (one to two years, three to four years and over four years) for 34 birds of known age. Age was neglected in further analyses as it had no effect on the nest defence intensity of the breeding male or female (Kruskal–Wallis test, male calls $\chi^2 = 1.48$, d.f. = 2, $n = 22$ and $p = 0.478$, male attacks $\chi^2 = 3.67$, d.f. = 2, $n = 22$ and $p = 0.159$, female calls $\chi^2 = 0.676$, d.f. = 2, $n = 12$ and $p = 0.713$ and female attacks $\chi^2 = 2.60$, d.f. = 2, $n = 12$ and $p = 0.272$). The defence intensities towards the models of the sparrow and dove were pooled for each individual and analysed for each sex with the Kruskal–Wallis test. Zero values were allocated to birds which were not present during the experiment. Means are expressed with standard errors.

3. RESULTS

(a) *Nest guarding behaviour*

Because the time allocated to nest guarding by the female and male was independent of the presence of helpers (Mann–Whitney test, female $U = 190.0$, $n_1 = 51$, $n_2 = 9$ and $p = 0.690$, and male $U = 334.5$, $n_1 = 51$, $n_2 = 9$ and $p = 0.241$), the nest guarding data for each island were combined. The amount of time spent nest guarding by female Seychelles warblers on Cousin and Aride Islands was low and similar (mean nest guarding, $0.3 \pm 0.1\%$ and $n = 36$ and $0.1 \pm 0.0\%$ and $n = 24$, respectively), whereas males on Cousin Island (with fodies) performed 4.8 times more nest guarding than males on (egg-predator-free) Aride Island (mean nest guarding $10.6 \pm 1.7\%$ and $n = 36$ and $2.2 \pm 0.9\%$ and $n = 24$, respectively) ($U = 236.5$ and $p = 0.003$).

(b) *Predator recognition: differences between models and islands*

The defence intensities of Seychelles warbler pairs towards the mounted sparrow and the caged fody were equal (mean number of calls per minute for sparrow versus fody, male 35.2 ± 5.7 versus 32.8 ± 4.1, $U = 62.0$, $n = 27$ and $p = 0.977$, and female 44.3 ± 5.3 versus 28.8 ± 8.9, $U = 45$, $n = 27$ and $p = 0.256$ and mean number of attacks per minute for sparrow versus fody, male 6.3 ± 2.2 versus 5.0 ± 1.4, $U = 52.0$, $n = 27$ and $p = 0.519$, and female 2.3 ± 0.8 versus 2.7 ± 0.5, $U = 54.0$, $n = 27$ and $p = 0.589$), indicating that the warblers perceived the mounted sparrow as a fody. In order to determine whether the warblers recognized the egg predator, we tested for differences in their defence intensities towards the three models and between Cousin and Aride Islands (figure 2). The warblers defended significantly more towards the sparrow than towards the dove (only once was a male warbler observed attacking the dove model). This was the case within each island (figure 2), but also with the data of both islands pooled (Wilcoxon signed-rank test, calls $Z = 3.95$, $n = 72$ and $p < 0.001$, and attacks $Z = 6.22$, $n = 72$ and $p < 0.001$). Both sexes of the warblers on Cousin Island responded significantly less intensively (calls and attacks) to the great tit than to the sparrow (figure 2). Their responses towards the great tit and the dove were similar (figure 2). The difference between defence against the sparrow and ground dove (proportional measure of defence) by warblers on Cousin and Aride Islands was identical (calls $U = 142.0$, $n = 36$ and $p = 0.634$ and attacks $U = 127.0$, $n = 36$ and $p = 0.340$) (see figure 2).

Because there was no effect of island on nest defence intensities, call and attack frequencies towards the sparrow on both islands were pooled for analysing sex-specific differences. The female call frequency was significantly higher (33.8%) than the male call frequency (female 36.4 ± 3.0 and male 27.2 ± 3.2), whereas the male attack frequency was significantly higher (95.0%) than the female attack frequency (male 7.8 ± 1.7 and female 4.0 ± 1.1) (figure 3).

4. DISCUSSION

(a) *Sex-specific, anti-nest predator behaviour*

Parents should optimize their nest guarding and nest defence behaviour in order to maximize their reproductive success (Andersson *et al.* 1980). Buitron (1983) argued that, in monogamous species with biparental care, both parents should invest equally in nest guarding and defence. This has been verified in some studies (e.g. Greigh-Smith 1980). However, our study on the Seychelles warbler and other studies (Smith *et al.* 1984; Breitwisch 1988; Weatherhead 1989; Gill & Sealy 1996; Hatch 1997) found sex differences in nest guarding and defence. Compared with their breeding partner, the male Seychelles warbler engaged in more nest guarding behaviour on Cousin Island where Seychelles fodies are present. Males are extremely effective at deterring

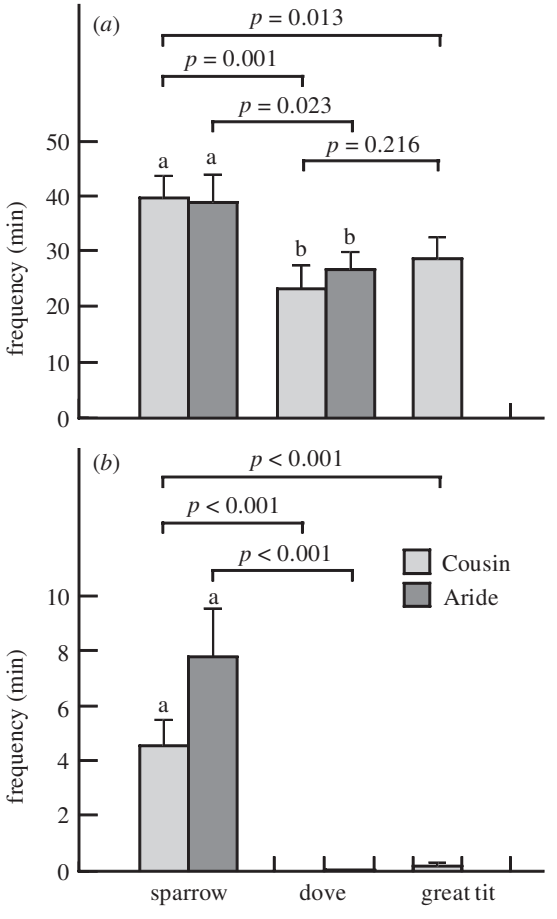

Figure 2. (*a*) Call and (*b*) attack rates of Seychelles warblers towards models of house sparrow and barred ground dove by Seychelles warbler breeding pairs (male and female combined) during incubation on Cousin and Aride Islands (no Wilcoxon signed-rank test between attack rates towards the models of the dove and tit because no attacks were observed towards the dove). Groups with the same letter are not significantly different.

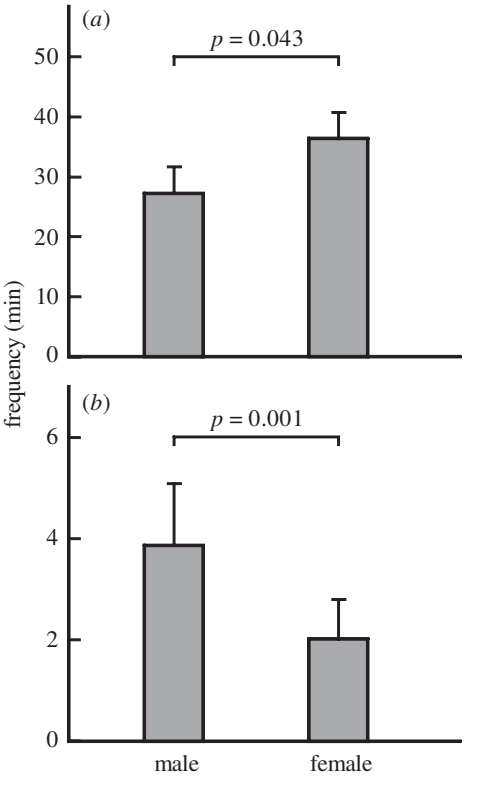

Figure 3. (*a*) Call and (*b*) attack frequency towards the sparrow model for male and female Seychelles warbler. The actual numbers of calls towards and attacks on the sparrow were used (only one attack towards the dove was observed and there was no correlation between the number of calls towards the sparrow and dove) ($r^2 = 0.001$, $n = 72$ and $p = 0.849$).

Seychelles fodies and egg loss (on islands with Seychelles fodies) is inversely related to the amount of nest guarding by males (Komdeur & Kats 1999). However, nest guarding is energetically costly and adjusted to the presence of predators (Komdeur & Kats 1999). Our study confirmed this plasticity in nest guarding behaviour. Males on Cousin Island spent significantly more time nest guarding than males on Aride Island, whereas the time spent nest guarding by females was low and similar on both islands. The Seychelles warbler had a significant, sex-specific difference in attack and call rate towards the stuffed female house sparrow, the fody surrogate. Compared with their breeding partner, the male engaged more in 'attack' behaviour while the female called more frequently. Because attacking is energetically more costly than calling (Montgomerie & Weatherhead 1988), male Seychelles warblers spend more energy in nest defence than females. Although females spent less time nest guarding, they may invest the same amount of energy in the clutch because they perform all the incubation (Komdeur & Kats 1999).

(b) *Predator recognition and anti-predator behaviour*

Experience with nest predators may influence the nest defence of individuals through learning (Williams 1966; Goodman 1974; Pianka & Parker 1975; Weatherhead 1989; Hakkarainen & Korpimäki 1994). Nest defence intensity (attack and call rates) towards the sparrow was equally high for warblers on Cousin Island and Aride Island (which had never had any experience with the predator) and independent of the warbler's age. The mounted sparrow was an accurate model for a fody because the warbler's nest defence intensity was equally as great towards the mounted sparrow as the caged fody. One could argue that the high level of defence towards the sparrow on Aride Island was due to unfamiliarity with the model. However, the experiments using the dove as a familiar bird and the great tit as a novel bird indicated that this is not the case. First, the proportional measure for the difference between defence against the house sparrow and the barred ground dove was similar for warblers on both Cousin and Aride Islands. Second, the attack frequency of the warblers towards the tit was low and significantly lower than that aimed at the house sparrow. Third, the defence intensity towards the great tit was similar to that directed towards the barred ground dove. The attack rate was significantly higher when directed towards the sparrow than to either of the other models. It would be beneficial to record the warbler's nest defence intensity towards a decoy of a novel species which is a common egg predator or a brood parasite of other *Acrocephalus* species. However, a European cuckoo (*Cuculus canorus*), which is a common brood parasite of other *Acrocephalus* species (Cramp 1985), was observed on four

occasions on Cousin Island within a 3 m radius of a warbler's nest containing a clutch. The warblers did not show any nest defence behaviour towards the cuckoo (J. Komdeur, personal communication). In conclusion, this study has demonstrated that the nest defence intensity directed towards the different model species is a result of the Seychelles warbler reacting to the different predation threats posed by the different model species presented and that predator recognition is innate and does not require specific experience with the predator.

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